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INFLUENCE OF EMBRYONIC METABOLIC RATE AND
INCUBATION TEMPERATURE ON INCUBATION LENGTH VARIATION
IN NEOTROPICAL PASSERINES

By

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Thesis presented in partial fulfillment of the requirements
for the degree of

Master of Science

in Wildlife Biology

The University of Montana
Missoula, MT

Fall 2007

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INFLUENCE OF EMBRYONIC METABOLIC RATE AND INCUBATION
TEMPERATURE ON INCUBATION LENGTH VARIATION IN NEOTROPICAL
PASSERINES

Chair: Thomas E. Martin

Variation in embryonic developmental periods influences fitness, but causes of interspecific variation are poorly understood. Allometry, for example, does not explain variation in incubation periods among neotropical passerines. Incubation temperature can explain some variation in developmental periods, but substantial variation remains unexplained. Here we examine two previously untested alternatives. Adult metabolic rates differ among species and similar differences among embryos may explain some variation in embryonic development rates; higher metabolism may allow faster cellular proliferation. Alternatively, metabolic rates are temperature dependent, and metabolic rates might respond differentially to temperature among species and compensate for differing incubation temperatures. These alternatives are untested across any taxa. Therefore, we examined them in tropical Venezuela by measuring embryonic metabolism at four temperatures in 15 passerine species with incubation periods ranging from 12 to 27 days. Embryonic metabolic rates responses to temperature were different among species even at constant embryonic age. Furthermore, species with lower average daily incubation temperature are less sensitive to changes in temperature than species with higher average incubation temperatures. Differences in embryonic mass specific metabolic rate among species explained a significant amount of variation in incubation periods after correcting for incubation temperature. Thus, differences in the “rate of living” as manifested through metabolism can influence developmental trajectories and deserve greater attention.

To: My parents Lalo and Ana, my brothers Edu, Juancho and Tomy and to my beloved grandparents Yeye, Tata y Marta.

Acknowledgments

Thank you Tom for all your support and the opportunity to become a better scientist. I am very grateful to my committee Winsor Lowe and Art Woods for their help in the development of this thesis. I want to thank my lab mates, Yi-ru Cheng, Brad Fedy, Brian Schwartz, Dan Barton, Amy Stokes, TJ Fontaine and Karie Decker for their friendship and helpful comments on this manuscript. Vanetta Burton: You are an amazing person, thank you for all your help, love and friendship. The TEA group especially Robert Fletcher, Cristine Miller and Elliot Parsons were very important in my development as a scientist. My friends Roman Ruggera, Petu Foguet, Daniel Munoz, William Goulding, Luis Biancucci, Jennifer Lang, Jemma Finch, Riccardo Ton, Andrew Hoar, Karolina Fierro-Calderon, Andrew and Alison Cox and Violeta Gomez Serrano made my 5 years of field work in Venezuela unforgettable. To Juan Palote, Jesus and Ambrosio park guards of the Yacambu National Park in Venezuela for their support and friendship. To Mary Kamensky of the Graduate School of the University of Montana for her invaluable help. My gratitude to all members of the Multicultural Toastmasters Club at the University of Montana for their friendship and their help in improving my communication skills. To my friends Becky and Grant Kier, Chris and Katherine Filardi, Rebecca and Magnus McCaffery, Claudia and Rafaela Castro, Michelle and Adina Rutherford, Heather Johnson, Julie Beston and especially Jose Hierro, Alex Fajardo, Hanna Golota and Jennifer Erickson thank you for such a wonderful friendship. Thank you M. Sanjayan for all your love and for being there for me, always. And to my four legged best friend Zafra that will always remind me of Venezuela and the amazing journey of being in Graduate School at the University of Montana.

Figure legends

Figure 1. Oxygen consumption rates [$\dot{V}\text{O}_2$ (mL h⁻¹)] during 2006 and 2007. Axes are on the same scale to allow comparisons of differences in extent of variation among years.

Each point represents a species.

Figure 2. Species oxygen consumption rate [$\dot{V}\text{O}_2$ (mL h⁻¹)] slopes in response to temperature. Each line represents a species.

Figure 3. Regression plot showing the relationship of average incubation temperature (24hr) and oxygen consumption rate [$\dot{V}\text{O}_2$ (mL h⁻¹)] slope among species in response to temperature.

Figure 4. Regression plot showing the relationship of egg mass and incubation period length among our study species.

Figure 5. Partial regression plot showing the relationship of mass corrected oxygen consumption rate and duration of incubation periods. Insert: shows the partial regression plot showing the relationship of average 24hr. egg temperature and duration of incubation periods. Each point represents a species

Introduction

Embryonic development is of great interest because it has critical consequences for phenotypic expression and offspring quality (Arendt 2000), ultimately, influencing fitness (Roff 1992). Conditions during development can affect growth rates, body size, metabolism, immunocompetence and sexual attractiveness and fecundity in adulthood (Arendt 1997; Brommer 2003; Hepp 2006; Billerbeck et al. 2001; Hare et al. 2004; Shine et al. 1997; Lindstrom 1999). Embryonic development periods (i.e. incubation period, gestation period) vary extensively within and among diverse taxa: placental mammal gestation length can vary from 18 to 660 days (Promislow and Harvey 1990) and incubation period of birds range from 9 to about 80 days (Rahn and Ar 1974; Lloyd 2004). Variation in development periods is typically attributed to allometric scaling, with larger species having longer developmental periods (Rahn and Ar 1974; Case 1978). Yet, birds represent a particularly interesting problem. Allometry does not explain interspecific variation in developmental periods for a large group of passerine species (Martin 2002, Martin et al. 2007). Consequently, interspecific variation in development periods in passerine species must be explained by other mechanisms that need identification.

Within species of true ectotherms and birds (bird embryos are effectively ectotherms during incubation), temperature affects the length of development periods (Boersma 1982, Deeming and Ferguson 1991) which can affect offspring size. For example, longer incubation periods and decreased offspring size and growth rates are associated with colder incubation temperatures in lizards (Hare et al. 2004), fish (Green and Fisher 2004) and turtles (Packard et al. 1987). However, long developmental periods

may increase offspring quality if temperature is held constant (Martin and Schwabl 2007). Yet, offspring quality may be compromised if these long developmental periods are the result of colder temperatures. Zebra Finch (*Taeniopygia guttata*) embryos experiencing colder temperatures during development hatched with smaller body size and had poor growth efficiency (Olson et al. 2006).

Differences in average incubation temperature can also explain interspecific variation in development periods in passerine species (Martin 2002, Martin et al. 2007). However, many species with similar average incubation temperatures still differed in incubation periods (Martin et al. 2007) and this variation remains to be explained.

Metabolic rates might explain variation in development rate among species, although this possibility is untested across species. Here, we test two alternatives that may explain interspecific variation in developmental rates. A) *Embryonic metabolic rate sensitivity to temperature*: metabolism provides the necessary energy for maintenance and tissue growth (Vleck et al. 1980, Hoyt 1987) and temperature influences how efficiently embryos can develop (Fleming and Gross 1990; Vleck and Vleck 1987; Olson et al. 2006). However species may evolve differing metabolic responses to temperature in relation to the temperatures they regularly experience. Bird species that experience lower nest attentiveness (time spent by the adult incubating) have lower average incubation temperatures (Martin et al. 2007) and may have evolved lowered sensitivity to temperature. Reduced sensitivity may be manifested as less reduction in metabolic rates with decreasing temperature as a measure of compensating for decreased attentiveness and temperature on development rate. Thus we predict that species with low daily average temperatures will have lower sensitivity to changes in temperature. B) *Species*

specific embryonic metabolic rate: adult metabolic rates differ among species (Faaborg 1977; Hails 1983; Prinzinger et al. 1995; Cierlik et al. 2004, Wiersma et al. 2007) and similar differences among embryos may explain some of the variation in developmental periods. Species with higher metabolic rates in embryos may have shorter developmental periods due to faster cellular proliferation (Arendt 2000). Thus, we tested the prediction that species with higher embryonic metabolic rates will have shorter incubation periods. These alternatives have not been tested across any group of taxa. Hence, we explored these alternatives by measuring embryonic metabolic rates of 15 neotropical passerine species at varying temperatures that embryos regularly experience during incubation in Venezuela.

Study Area and Methods

Field work was conducted at Yacambú National Park, a montane cloud forest area in north-central Venezuela (09° 42' N, 69° 42' W) (see Fierro-Calderón and Martin 2007 for details of area). The study area was searched for bird nests between 1,350 and 2,000 m during the entire breeding seasons of 2006 and 2007.

Nests were monitored following long term protocols (Martin 1998, 2002; Martin et al. 2000). Nests were checked every two to four days to determine status, but were checked daily or twice daily near stage-changing events such as hatching to accurately measure period duration. Duration of incubation was measured as the number of days between the last egg laid and the last egg hatched (Nice 1954; Briskie and Sealy 1990; Martin et al 2007).

Egg Temperature

Egg temperatures were measured on the first or second day of incubation by inserting thermistors into the center of eggs through a small hole sealed with glue (Weathers and Sullivan 1989; Martin et al. 2007). The wire was threaded through the nest and connected to a HOBO Stowaway XTI datalogger (Onset Inc., Bourne, MA, USA) which recorded temperatures every 12 - 24 s for five to eight days per nest. We used data from days two to six to standardize sampling and minimize possible disturbance effects on the first day. We excluded nests where temperatures systematically changed from failing batteries or poorly sealed holes (Martin et al. 2007). Egg temperature data for two species (*Thraupis episcopus* and *Tachyphonus rufus*) included in this study were not included in previous analyses (Martin et al. 2007). Temperature data are included to separate their effects from metabolic effects in our analysis.

Embryonic metabolic rate

One of the most common measures of metabolic rate is oxygen consumption rate [$\dot{V}O_2$ (mL h⁻¹)] (Schmidt-Nielsen 1997). Embryo $\dot{V}O_2$ was measured when 45% to 90% of the incubation period had been completed. To examine differences among species in metabolic rate responses to temperatures we measured $\dot{V}O_2$ at four temperatures (37.5, 31, 23.5 and 17 °C). These temperatures were selected to represent the range of temperatures that embryos regularly experience during incubation based on egg temperature sampling (see *Egg Temperature*).

Eggs used for measurements were removed from the nest, replaced with fake eggs, immediately taken to the field station and returned to their nests after $\dot{V}O_2$ measurements. In 2006, each egg was randomly assigned to only one temperature of the

set: 37.5, 31, 23.5 or 17 °C to measure embryonic $\dot{V}O_2$. No egg was measured at any other temperature than the designated one. The egg was placed in a plastic syringe used as a metabolic chamber, and let rest for 60 min to compensate for any mechanical stress the embryo might have suffered during the transportation process. Subsequently, the syringe was flushed with air at ambient temperature, sealed, and immediately submerged in a temperature controlled water bath set at the testing temperature assigned for that egg. The amount of time the egg spent in the water bath varied from 35 to 120 min, with older and bigger eggs taking longer time than younger and smaller eggs to decrease the oxygen concentration to a measurable level (following Olson et al. 2006). Afterwards, the syringe was taken out of the water, the outlet opened, and a known volume of the gaseous environment within the syringe was washed out into an open flow system for O₂ concentration analysis. Oxygen concentration was measured using a FoxBox (Sable Systems Inc. oxygen analyzer, Las Vegas, NV, USA). The amount of O₂ exchanged was determined by integrating the area below the O₂ concentration vs. time curves, for which the initial and final dry air values served as baseline. $\dot{V}O_2$ (reported at standard temperature (0 °C), 1 atm pressure, and dry (std)) was determined by dividing the integrated values by the total time of the syringe closure (following Gefen and Ar 2001). We assumed that the oxygen consumption recording interval represents the “long-term” metabolic activity for that stage of development and temperature (Olson et al. 2006).

In 2007 the embryonic $\dot{V}O_2$ of each egg was measured in an open flow system in a continuous sequence of temperatures in the following order: 37.5, 31, 23.5 and 17 °C. This temperature sequence represents the range of temperatures that embryos regularly experience during incubation based on egg temperature sampling (see *Egg Temperature*).

Each egg upon arrival to the field station was immediately placed in a metabolic chamber connected to an open flow system and submerged in a water bath set at the first temperature of the sequence. O_2 consumption rate was measured continuously every 0.5 sec. and changes observed as the embryo equilibrated at each temperature. Once the O_2 concentration reached a plateau the metabolic chamber was submerged into the next water bath in the temperature sequence. $\dot{V}O_2$ (mL h⁻¹) was calculated using the O_2 concentration value at the plateau of each temperature.

Egg mass and egg volume

Eggs were weighed after each metabolic measurement using an ACCULAB portable electronic scale (precision 0.001 g) (Edgewood, NY, USA). Egg length and width was measured using Mitutoyo digital calipers (precision 0.01 mm) (Kawasaki, Japan). Volume was estimated using Hoyt's (1979) formula ($0.51 \times \text{length} \times [\text{width}^2]$).

Data analysis

Embryonic metabolic rate and temperature

To examine embryonic metabolic responses to different temperatures we used a General Linear Model (GLM) with square-root-transformed $\dot{V}O_2$ as the dependent variable. Slopes of $\dot{V}O_2$ relative to temperature within species were compared across species as a test of embryonic metabolic rate sensitivity to temperature. To obtain each species slope, we first used a GLM with square-root-transformed $\dot{V}O_2$ as the dependent variable, species as a fixed factor and embryo age as a covariate. Individual egg identity was included as random effect to control for the independence of measurements of the same egg. The standardized residuals for square-root-transformed $\dot{V}O_2$ obtained from the GLM were used in a linear regression with water temperature as the independent variable

and the standardized residuals for square-root-transformed $\dot{V}\text{O}_2$ as dependent variable to obtain each species slope. We used a linear regression with species slope value as the dependent variable and average incubation temperature (24hr) as the independent variable to examine the sensitivity of each species to incubation temperature.

Egg mass and incubation period

We examined the ability of egg mass to explain incubation period length using a linear regression analysis with incubation period length as dependent variable and the least squares mean estimates of egg mass for each species (controlling for embryo age) as the independent variable.

Embryonic metabolic rate and incubation period

We used a multiple regression approach to examine the ability of mass-specific $\dot{V}\text{O}_2$ to explain interspecific variation in incubation periods after correcting for average incubation temperature (24hr). We obtained least squares mean estimates of $\dot{V}\text{O}_2$ for each species from a GLM that used square-root-transformed VO_2 as the dependent variable, species and water temperature as fixed factors and embryo age (measured as percentage of the total incubation period on the day of measurement) as a covariate. Individual egg identity was included as random effect to control for the independence of measurements of the same egg. We calculated mass-corrected $\dot{V}\text{O}_2$ for each species by dividing the least squares mean estimates of $\dot{V}\text{O}_2$ by the least squares mean estimates of egg mass for each species (controlling for embryo age). We used incubation length (in days) as the dependent variable and mean incubation temperature (24hr) and mass-specific $\dot{V}\text{O}_2$ as independent variables. All statistical analyses were performed using SPSS 12.0.

Results

. Our study species from nine avian families (Appendix) provided a wide range of incubation periods from 12 to 27 days. A total of 191 and 251 embryonic metabolic rate measurements were performed during 2006 and 2007, respectively.

We checked the consistency of oxygen consumption measurements between years because we used two different procedures. Measurements were highly correlated ($r = 0.85$, $P = 0.001$, Fig. 1) and did not differ between years ($t_{(20)} = -1.531$, $P = 0.141$). Therefore, we pooled years to increase the number of species. However, it is important to note that the methodology used during 2006 underestimated $\dot{V}O_2$ values. This resulted from including in our calculations O_2 consumption values during embryonic equilibration to the designated experimental water bath temperature. We are currently working on a methodology that will correct these errors in $\dot{V}O_2$ calculations.

Embryonic metabolic rate and temperature

Species differed in their embryonic $\dot{V}O_2$ among temperatures, even after controlling for embryo age, and species differed in the rate of change in slope of $\dot{V}O_2$ with temperature (species: $F_{14,250} = 13.24$, $P < 0.001$; temperature: $F_{3,250} = 1012.16$, $P < 0.001$; embryo age: $F_{1,250} = 375.11$, $P < 0.001$; and species x temperature: $F_{38,250} = 5.73$, $P < 0.001$). The interaction of species with temperature was orderly with all species showing positive slopes (Fig. 2). The positive interaction of species with temperature indicates that all species increased metabolism at higher temperatures but have different slopes. The rate of change in $\dot{V}O_2$ with temperature followed our prediction; it was greater in species with higher daily average incubation temperatures than in species with

lower average daily incubation temperature. Species with the steepest slopes are the most sensitive to temperature ($r = 0.635$, $P = 0.011$, Fig. 3).

Egg mass and incubation period

We found no relationship between egg mass and incubation period length variation ($r = .030$, $P = 0.28$, Fig. 4). This result is similar to the one previously found by Martin et al. (2007).

Embryonic metabolic rate and incubation period length

Species differed in metabolic rates for a given temperature and age (see above). Mass-specific $\dot{V}O_2$ of species explained variation in incubation periods ($(r_p = 0.606$, $P = 0.022)$ (Fig. 5)) after correcting for daily average incubation temperature ($(r_p = 0.931$, $P < 0.001)$ (see insert on Fig. 5)).

Discussion

Embryonic growth rate and metabolic rate increase continuously during incubation in altricial species (Vleck and Vleck 1987) and increases with temperature. The positive interaction of species with temperature indicates that all species increased metabolism at higher temperatures (Figs. 2, 3). These differences remained even when controlling for embryo age effects. Species may vary in evolutionary solutions and extent of physiological trade-offs in embryonic development (Martin et al. 2007). Our results indicate that species have evolved different metabolic responses to cope with temperatures regularly experienced during incubation. Species with lower average daily incubation temperatures are the least sensitive to changes in temperature indicating that they may have lower “optimum” development temperatures than species that have higher incubation temperatures. This differential sensitivity to temperature could be achieved

through biochemical adaptations at the sub-cellular level. Changes in protein and enzyme structure and activation energies, PH levels, cell membrane diffusion properties as well as its transport proteins (chaperons) may enable the embryo to cope with low average incubation temperatures and increase metabolic efficiency (Olson et al. 2006; Hochachka and Somero 2002). A very interesting possibility worth exploring is the ability of embryos to defer tissue growth until late in incubation to minimize tissue maintenance costs hence reducing the total energy cost of development (Vleck and Vleck 1987).

We bring a new perspective in understanding interspecific variation in incubation period by showing for the first time that differences in embryonic mass-specific metabolic rate among species explains a significant amount of variation in incubation periods after correcting for incubation temperature (Fig. 5). Species with longer incubation periods (for a constant temperature) are thought to have slow development rates to be able to increase immune competence (Ricklefs 1992; Tieleman et al. 2005), increase nestling quality (i.e. better nervous and digestive systems) and increase longevity (Ricklefs 1992, Ricklefs and Starck 1998). In species with particularly high adult survival rates and long incubation periods, low mass-specific metabolic rates may allow embryos to develop higher quality systems. This could be the case for the Spotted Barbtail (*Premnoplex brunnescens*) which has the longest incubation period (27d) and the lowest mass specific metabolic rate of all our study species. Comparisons on energetical content of eggs at the time of laying with residual egg yolk and hatchling mass are needed to have a better understanding of the influence of embryonic metabolic rates and incubation temperature on nestling quality.

Underlying variation in life-history traits is a key step in advancing understanding of life-history evolution (Schwabl et al. 2007) and our study is the first to demonstrate that differences in the “rate of living” as manifested through metabolism can greatly influence developmental trajectories and deserve further investigation.

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Appendix. List of species included in this study

Phylogenetic group	Scientific name	Four letter code
Thraupidae	<i>Thraupis episcopus</i> *	PATA
Thraupidae	<i>Tachyphonus rufus</i> *	WLTA
Emberizidae	<i>Atlapetes semirufus</i>	OBBF
Parulidae	<i>Basileuterus tristriatus</i>	TSWA
Parulidae	<i>Myioborus miniatus</i>	STRE
Troglodytidae	<i>Henicorhina leucophrys</i>	GBWW
Turdidae	<i>Turdus olivater</i>	BHTH
Turdidae	<i>Platycichla flavipes</i>	YLTH
Turdidae	<i>Catharus aurantiirostris</i>	OBNT
Turdidae	<i>Catharus fuscater</i>	SBNT
Furnariidae	<i>Premnoplex brunnescens</i>	SPBA
Thamnophilidae	<i>Myrmotherula schisticolor</i> †	SLAN
Thamnophilidae	<i>Dysithamnus mentalis</i> †	PLAN
Tyrannidae	<i>Mionectes olivaceous</i>	OLFL
Formicariidae	<i>Grallaricula ferrugineipectus</i>	RBAN

† Species only measured in 2006

* Species only measured in 2007

Fig. 1

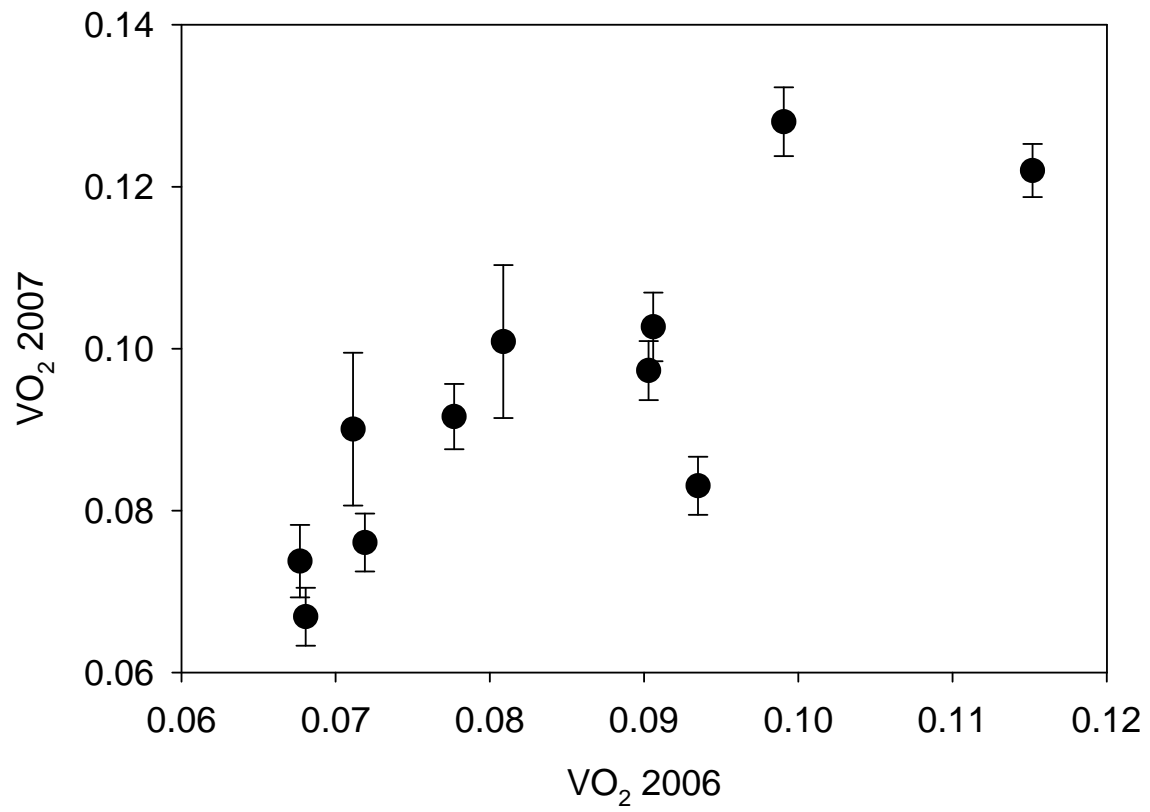


Fig. 2

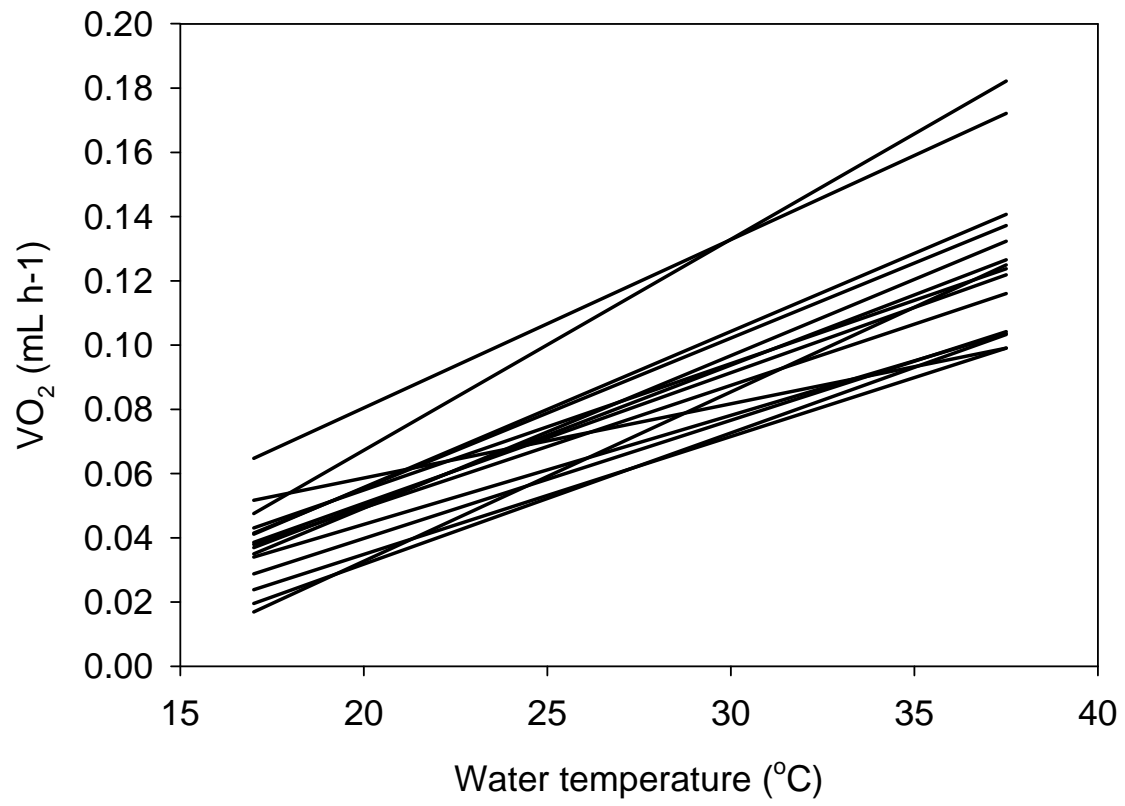


Fig. 3

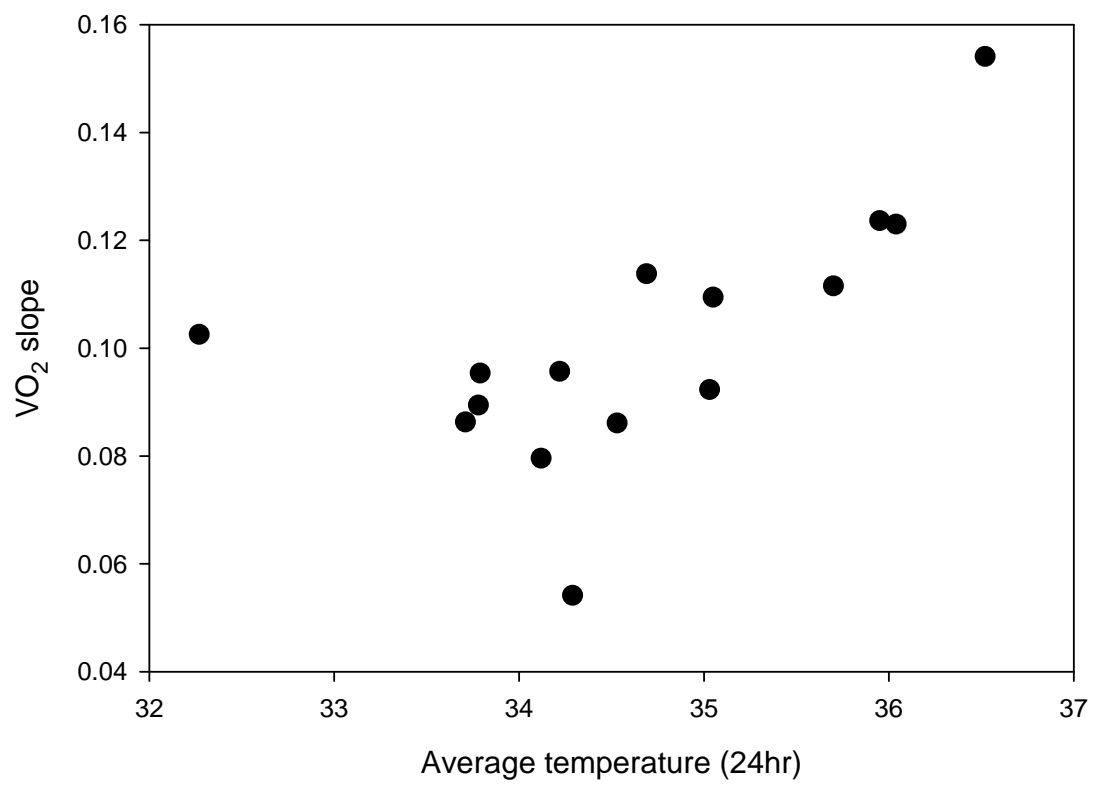


Fig. 4

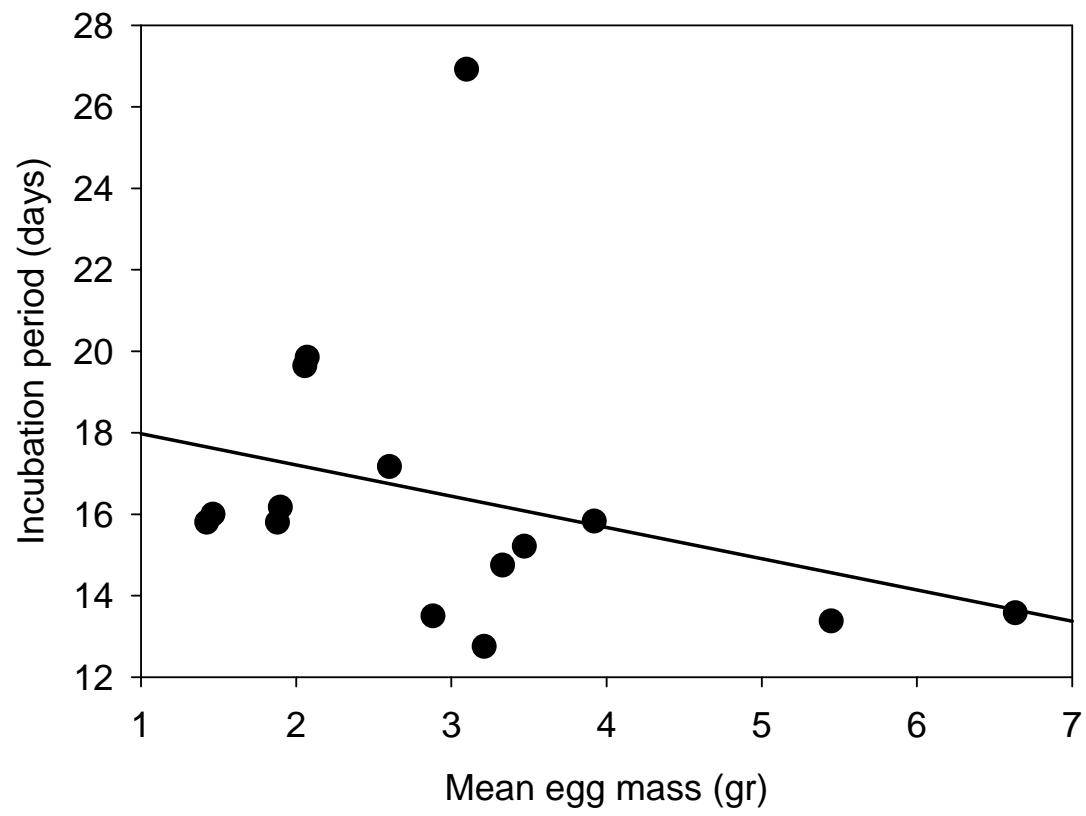


Fig. 5

